What controls the freshwater fish fossil record? A focus on the Late Cretaceous and Tertiary of Afro-Arabia

by

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ABSTRACT. - The aim of this paper is to define the constraints by geology, climate, and eustasy on the freshwater fish fossil record through a qualitative analysis. The impact of these factors on the access to and knowledge of the freshwater fish fossil record is also evoked. The focus is on Afro-Arabia for the last several 100 million years, which corresponds with the rise and diversification of the modern fish fauna on the continent. After a review of the main environmental changes recorded in Afro-Arabia through this time span, I briefly present the history of fish fossil record and the distribution of the associated fossiliferous sites. Then, effects of environmental factors on the freshwater fish fossil record are described and discussed through case studies. Depending on the size of the drainage system, the fossil taxonomic richness varies notably in relation with the hydrodynamism of the environment. Second, freshwater fish outcrops are associated with an increase in accommodation in all case studies. Moreover, environmental factors delimit our knowledge of the fossil record. To increase this knowledge, we have to prospect previously neglected areas but we also may give more attention to small fraction size fossils and to isolated bones.

RÉSUMÉ. - Qu'est-ce qui contrôle le registre fossile des poissons d'eau douce? Focus sur le Crétacé supérieur et le Tertiaire de l'Afro-Arabie.

L'objectif de cet article est de définir les contraintes exercées par la géologie, le climat, l'eustasie sur le registre des poissons d'eau douce, à travers une analyse qualitative. L'impact de ces facteurs sur l'accès et la connaissance de ce registre fossile est aussi estimé. La zone d'intérêt et la période de temps considérées sont l'Afro-Arabie pendant les 100 derniers millions d'années, ce qui correspond à l'émergence et la diversification de l'ichtyofaune moderne sur cette plaque continentale. Après la revue des principaux changements environnementaux enregistrés en Afro-Arabie pendant ce laps de temps, je présente une courte histoire de la découverte des poissons fossiles et la distribution des sites associés. Ensuite les effets de facteurs environnementaux sur le registre fossile des poissons d'eau douce sont décrits et discutés à partir de cas d'étude choisis. Selon la taille du bassin drainant, la richesse taxinomique fossile varie, en particulier en lien avec l'hydrodynamisme du milieu. Les sites à poissons d'eau douce fossiles sont associés à l'augmentation de l'accommodation dans tous les cas étudiés. Enfin, l'environnement influence notre connaissance du registre fossile. Pour l'augmenter, nous devons prospecter les zones toujours négligées, mais aussi porter une attention accrue aux micro-restes et aux os isolés.

Key words. - Freshwater fish - Fossil record - Afro-Arabia - Tectonics - Climate - Accommodation.

The fossil record is the raw material used by palaeontologists to make their contribution to the knowledge of evolution. Intuitively, one may identify two types of factors that control the fossil record of fish.

The first type depends on the fish itself. The ability of a fish to enter the fossil record and the systematic information carried by the fossil remains depend on the taxon (its ecology, its distribution, the stoutness of the bones, etc.). In that sense, from a same community, some fish will be better preserved than others and one may predict the main features of the fossil assemblage that would result from its fossilization (Otero *et al*., in press). For instance, most of the African fossil catfish are those with strong dermal ossification of their neurocranium and with stout pectoral and dorsal spines. Such an ossification usually happens in only one genus (sometimes two genera) of each familial or sub-familial catfish group, of which the neurocranium anatomy is characteristic, such as *Clarias* and *Heterobranchus* in the family Clariidae. Indeed, the known fossil clariids belong to one or the other of these two genera, and so far no fossil has been reported in a clariid genus with a weaker ossification of the skull. Moreover, the part of the past diversity from environments with a scarce fossil record (due to a small extent and/or a low ability to be preserved) remains largely unknown, when compared with fish from environments that are commonly fossilized. For example, all clariid fossils have been recovered associated with fluvio-lacustrine or a fluvio-deltaic environments, whereas no clariid inhabiting caves has been sampled. Finally, a few bony characters only permit *Clarias* to be distinguished from *Heterobranchus*, and none is known to distinguish among *Clarias* species. As a consequence, the apparent diversity of a fossil assemblage with fossil clariids might be under-evaluated (see Otero *et al*., in press, for a discussion of a case study).

The second type of factor that constrains the fossil fish record is environmental *sensu lato* (if not otherwise noted,

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Cybium 2010, 34(1): 93-113.

the words "environment" and "environmental" refer to this meaning; conversely the cases of peculiar depositional, sedimentary, and diagenetic environments are clearly indicated). According to the environment, its extent, and the geological context (including tectonics and variation of the base-level) the record is favoured or not. This includes the sedimentary environment and the deposit dynamic, according to which the taphonomic processes differ, which induces a wide variety of fossil assemblages, according to whether or not the material is disarticulated, the preferential selection of size or density categories, and whether or not calcitic structures are preserved, among others. So, depending on the region and the time period, the environmental factors may play in different ways and could possibly obscure or emphasize certain aspects of the fish history: they control the freshwater fossil record itself.

Moreover, these environmental factors, notably those that operate at the time of fossilization, may impact at least partially our ability to identify the taxa. Together with the geological history of the region and the modern environment (including topography, vegetation, soil cover, and human activity) that combined in shaping our access to the potential fossil outcrops, they influence our knowledge of the freshwater fossil record.

That the environment controls the fossil record and also our knowledge of it has been long established and discussed. However, most of the studies concern the fossil record of marine animals, its relationship with sedimentary process

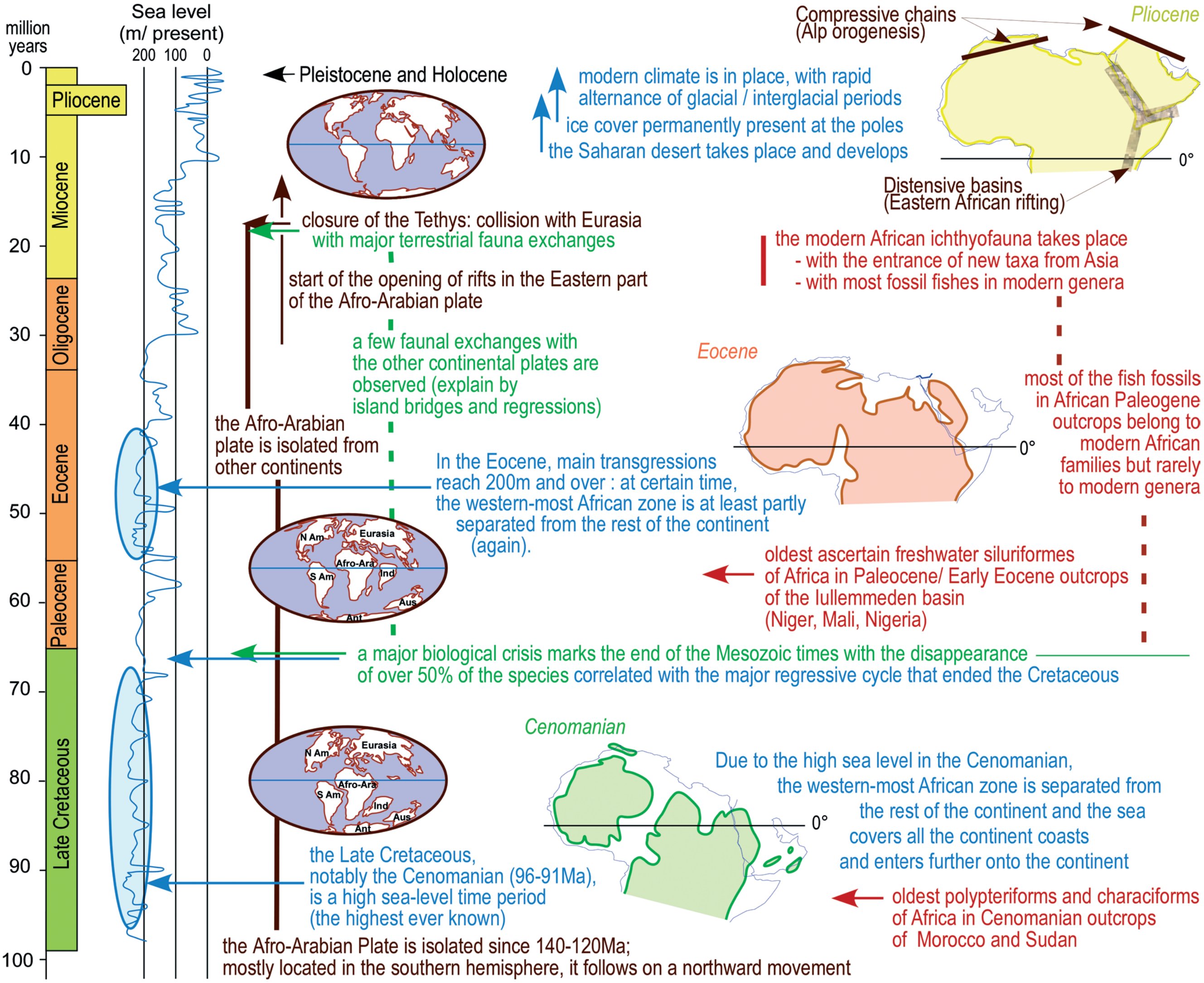
million years
Sea level (m/ present)
200 100 0
0
10
20
30
40
50
60
70
80
90
100
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Late Cretaceous
Pleistocene and Holocene
modern climate is in place, with rapid alternance of glacial / interglacial periods
ice cover permanently present at the poles
the Saharan desert takes place and develops
Compressive chains (Alp orogenesis)
Pliocene
0°
Distensive basins (Eastern African rifting)
closure of the Tethys: collision with Eurasia
with major terrestrial fauna exchanges
start of the opening of rifts in the Eastern part of the Afro-Arabian plate
the modern African ichthyofauna takes place
- with the entrance of new taxa from Asia
- with most fossil fishes in modern genera
a few faunal exchanges with the other continental plates are observed (explain by island bridges and regressions)
Eocene
0°
most of the fish fossils in African Paleogene outcrops belong to modern African families but rarely to modern genera
the Afro-Arabian plate is isolated from other continents
In the Eocene, main transgressions reach 200m and over : at certain time, the western-most African zone is at least partly separated from the rest of the continent (again).
N Am
Eurasia
Afro-Ara
S Am
Ind
Aus
Ant
oldest ascertain freshwater siluriformes of Africa in Paleocene/ Early Eocene outcrops of the Iullemmeden basin (Niger, Mali, Nigeria)
a major biological crisis marks the end of the Mesozoic times with the disappearance of over 50% of the species correlated with the major regressive cycle that ended the Cretaceous
Cenomanian
N Am
Eurasia
Afro-Ara
S Am
Ind
Aus
Ant
Due to the high sea level in the Cenomanian, the western-most African zone is separated from the rest of the continent and the sea covers all the continent coasts and enters further onto the continent
0°
the Late Cretaceous, notably the Cenomanian (96-91Ma), is a high sea-level time period (the highest ever known)
oldest polypteriforms and characiforms of Africa in Cenomanian outcrops of Morocco and Sudan
the Afro-Arabian Plate is isolated since 140-120Ma; mostly located in the southern hemisphere, it follows on a northward movement

Figure 1. - Main geological (brown), eustatic and climatic (blue), and biological (green) features of continental Africa through the last 100 million years with some associated fish bio-events (in red). The palaeogeographic maps show the relative positions of continents and the coastline of the northern half of Africa. Data are cited in the text, except the age of the stratigraphic limits found here and elsewhere in the text that are from the Chart of the International Commission on Stratigraphy (Gradstein *et al*., 2004).

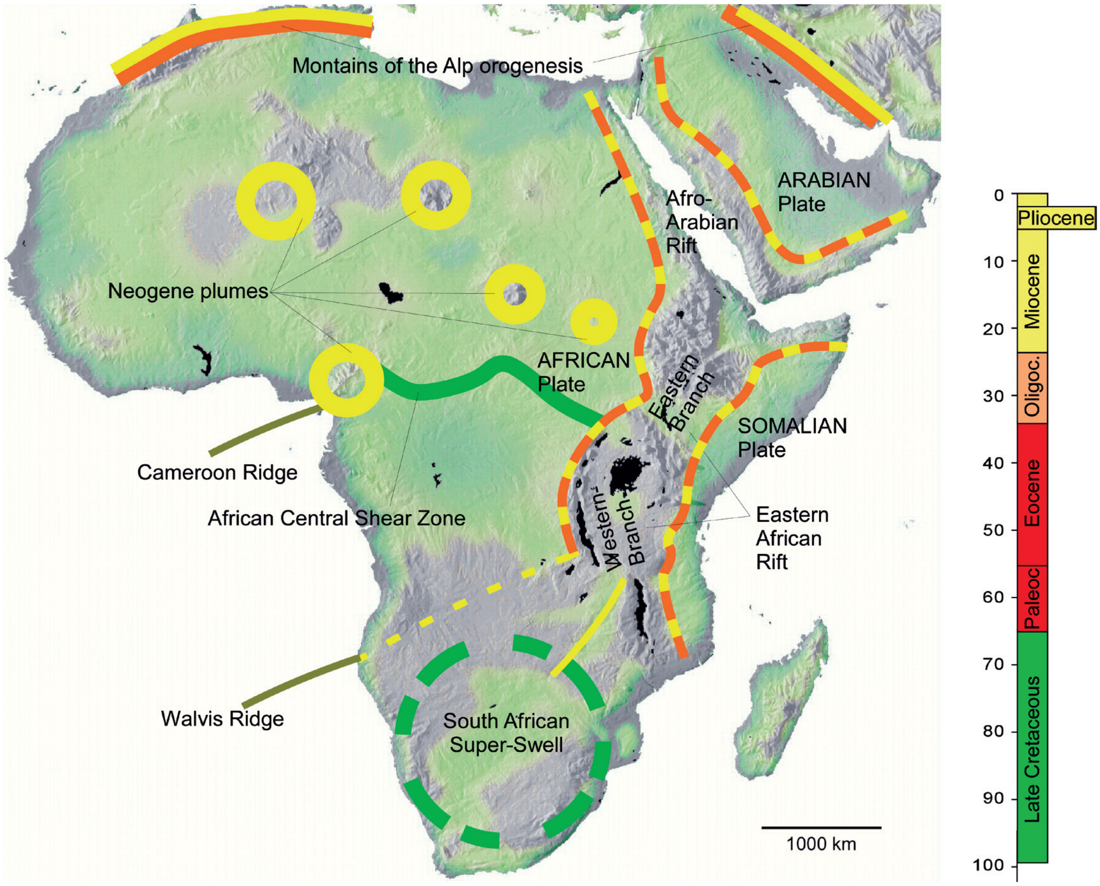

Figure 2. - Tectonic activity and anorogenic crustal movements since the Late Cretaceous shown on the modern topography of Africa. Data are cited in the text.

and sea-level change, the modelling of this relation, and the impact on evolutionary analyses (e.g., Kidwell, 1985, 1991, 1993; Brett, 1995; Holland and Patzkowsky, 1999; Smith, 2001; Smith *et al.*, 2001; Kidwell and Holland, 2002; Holland, 2003; Peters, 2006; Smith, 2007; Peters *et al.*, 2009). In continental areas the studies of the fossil record concentrate on tetrapods, which are mostly terrestrial (e.g., Benton, 1989; Fara and Benton, 2000; Fara, 2002). Indeed, how environmental factors impact the freshwater fish fossil record have not been evaluated so far at a large scale.

In this paper, I propose the first large scale review in both time (100 million years) and space (continental plate) of the freshwater fish fossil record in relation to the aspects of the environment that may impact the fossil record itself and also the understanding of and accessibility to it today (aquatic palaeoenvironment, fossilization context including local sedimentation, climate and regional geology, geological history, and modern environment). The multiplicity of the environmental factors affecting continental areas and their non-linear evolution through time makes it presumptuous to start with a quantification of their impact on the fish fossil record. This supposition fits with the conclusions of Fara (2002) when he tested the correlation between the fossil record (for continental tetrapods) and eustasy through the Cretaceous and the Cenozoic. Rather, the analysis proposed here is qualitative. It aims at defining the potential roles played by geology, climate, and eustasy in shaping the freshwater fish fossil record and at understanding the ways in which they constrain our knowledge of past diversity of fish. The present study may provide a first step guide to the choice of the cases to be studied to test the environmental factors separately. The focus is on the Afro-Arabian continental plate for the last 100 million years, that is, the Late Cretaceous and the Cenozoic. This time span corresponds to the rise and diversification of the modern fish fauna on the Afro-Arabian plate, as the oldest characiforms and polypteriforms are known in Cenomanian outcrops (99.6 Ma to 93.5 Ma, Fig. 1). They are the oldest occurrences of modern African fish orders.

During the last 100 million years, Afro-Arabia has seen a wide range of climatic and eustatic changes, such as the Late Cretaceous and Palaeogene marine transgressions (Haq *et al.*, 1987) and Neogene aridification in the subtropical zones in correlation with the onset of the glacial climate regime (Kennett, 1995, Burckle, 1995). Due to its geological structure and global tectonics, Afro-Arabia offers a variety of sedimentary settings where fish may have fossilized, from narrow rift basins to large epicontinental ones. Conversely, it shows a rather simple palaeogeographic history. Indeed, the Afro-Arabian plate remains isolated from other land masses since the dislocation of western Gondwana (achieved 100 Ma ago, e.g., Dercourt *et al.*, 2000) until the connection with Eurasia in the Early Neogene (about 20 Ma ago, e.g., Dercourt *et al.*, 2000). Despite the physical isolation of the plate some faunic exchanges are recorded, notably with Eurasia (Gheerbrant and Rage, 2006). A few fish taxa are concerned (Otero and Gayet, 2001; Otero *et al.*, 2008a).

To achieve my aim, I present the Afro-Arabian geology and fish palaeontology for the last 100 Ma: the environments (geology, climate) parallel to the freshwater fish evolution, the history of the fossil description, and the distribution of fossiliferous sites. Then, I propose an analysis of how environmental factors may shape the fish fossil record through case studies. Finally I also discuss how environmental factors can control the quality of our knowledge of this fossil record.

THE CONTEXT: THE GEOLOGY, THE CLIMATE, AND THE FISH

In this section, I review current knowledge on large-scale Afro-Arabian environmental history and the main features of the freshwater fish evolution during the last 100 Ma. The groups concerned in this section and more generally in the paper are the freshwater fish taxa that are present in Afro-Arabian outcrops since the Late Cretaceous. These are the dipnoan protopterids, the actinopterygian polypterids (Cladistia), and numerous actinopterygian teleostean taxa, most of which have extant members (for a synthesis of the modern African freshwater ichthyofauna, see for instance Roberts, 1975; Greenwood, 1983; Lévêque, 1997). The palaeomaps, time scales, and sea-level curves given in the figures of this section and elsewhere in the paper are for use as a guide. They correspond to current hypotheses and/or data syntheses, while further details and more references are to be found in the original papers cited in the text.

Dislocation tempo of the Afro-Arabian plate, connection with other plates, and faunal exchanges

The Afro-Arabian plate history starts by the end of the Early Cretaceous with the end of the Gondwana dislocation when it diverged from the South-American plate. The dislocation paroxysm was reached between 140 Ma and 120 Ma and the separation is generally considered to have been achieved 100 Ma ago (Dercourt *et al.*, 2000). At the beginning of the Late Cretaceous (which starts 99.6 Ma ago), the Afro-Arabian plate was isolated from the other continents by an oceanic crust and was bordered by passive margins only, in the Indian Ocean to the east, in the Atlantic to the west, and also by the Tethys that was still open to the north (Fig. 1; Dercourt *et al.*, 2000). The Afro-Arabian continent then remained separated from the other continental plates until the Neogene (23.0 Ma-present), when it contacted Eurasia at the north. However, the physical isolation of the plate does not correspond to a total isolation of the faunas. Interestingly, after its separation from South America, Afro-Arabia appears more strongly related to Laurasia than to any other Gondwana derived continent, whereas Madagascar, South America, and the Indian sub-continent appear to maintain tight faunal links until perhaps during the Late Cretaceous (e.g., Sampson *et al.*, 1998; Van Bocxlaer *et al.*, 2006; Krause *et al.*, 2006; Pereda-Suberbiola, 2009). The relationships and successive immigrations of mammalian (mostly placental) clades into Afro-Arabia allowed Gheerbrant and Rage (2006) to recognize five to seven phases of trans-Tethyan dispersal between that plate and Laurasia. They range from the Late Cretaceous to the Eocene-Oligocene transition (33.9 Ma). Gheerbrant and Rage (2006) also noticed that dispersals from Afro-Arabia to Laurasia were less numerous than those to Afro-Arabia and that they comprise only non-mammalian taxa. Among actinopterygian fish, alestid-like characiforms are present in certain European outcrops since the Campano-Maastrichtian and their highest known diversity in Europe at the Ypresian (55.8 Ma-48.6 Ma) correlates with the mammalian main dispersal phase from Afro-Arabia to Laurasia (Otero *et al.*, 2008a). Indeed, while I do not exclude that there is a single European lineage of characiforms since the Maastrichtian, their past diversity on this continent might be explained by successive trans-Tethyan dispersals (Otero *et al.*, 2008a). More generally, throughout the Late Cretaceous and most of the Cenozoic, fish invasions from South America and Europe to Afro-Arabia are scarce and their success on this continent has not been demonstrated so far. In that context, during isolation, Afro-Arabian freshwaters were mainly, if not only, inhabited by descendants from the former West-Gondwana stock and by some marine fish that adapted to freshwaters (e.g., Latidae, Otero, 1997). During about 80 Ma, changes in the intra-continental drainage system, in relation with climate changes and geological evolution, has driven the diversification of the freshwater fish that did not suffer any invasion from outside Afro-Arabia until the collision with Eurasia about 20 Ma ago.

The Late Cretaceous and the rise of the “African-type” ichthyofauna

Little is known about the Late Cretaceous (99.6 Ma-65.5 Ma) intra-continental topography of Afro-Arabia. Indeed the continent appears to have been a rather stable cratonic area during that time range (Goudie, 2005). The few topographic reliefs might be mainly those due to the Atlantic rifting along the western margin of the continent, notably south of the Walvis Ridge (Fig. 2; Séranne and Anka, 2005), and the African Central Shear zone. This latter east–west structure that currently still separates the Nilo-Sudan zone and the Congo basin is due to transtensive constraints in relation with the dislocation of Western Gondwana (Fig. 2; e.g., Goudie, 2005; Séranne and Anka, 2005; Stankiewicz and de Wit, 2006). The Southern African super-swell also probably takes place in the Late Cretaceous (*ibidii*). North, the Late Cretaceous is characterized by a low tectonic activity and a marine transgression over Northern and Western central Africa (Guiraud *et al*., 2005) until the Santonian stage (ca. 85.8 Ma to 83.5 Ma). Since the Santonian, the opening and the spreading of the Atlantic coupled with new convergent movement of Eurasia and Afro-Arabia were responsible for reorganization in the geodynamic constraints in the further Mediterranean zone, notably with the Syrtan basin opening at the beginning of the Cenozoic (Capitanio *et al*., 2009; Swezey, 2009) and more generally with the first compressional episodes registered by the Afro-Arabian plate during the Alpine Cycle (Guiraud *et al*., 2005).

Indeed, Late Cretaceous environmental change in Afro-Arabia appears to be due to climate and eustasy rather than to tectonics and geomorphology: the high sea-levels reached are the highest recorded in Earth history, particularly at the paroxysm of the Cenomanian transgression (Fig. 1; Haq *et al*., 1987). A large part of modern continental Afro-Arabia was submerged, notably in Northern and central Africa. The Afro-Arabian coasts were far inland and a wide marine corridor separated Western Africa from the remaining part of the continent and linked the Tethys and the South Atlantic (Fig. 1). Globally, great ichthyological renewal occurred before and just after the Cenomanian transgression (McLeod *et al*., 1997). In Afro-Arabia, this renewal corresponds to the first occurrence of polypteriforms and characiforms (Fig. 1; e.g., Dutheil, 1999a, 1999b). This is the first occurrence of freshwater fish that belong to actinopterygian orders still present in Africa today (the Arabian ichthyofauna is relictual) and most of them are descendants of the former West Gondwana stock such as characiform and siluriform fish. Indeed, as noticed by Cavin *et al*. (2001), the Cenomano-Turonian time period is marked by the characterization of both African and South American fish assemblages in relation with the opening of the South Atlantic.

The Cenozoic transition to modern Afro-Arabia and its fish fauna

Globally, the end of the Cretaceous was marked by a great regression, an increase in volcanism, and a mass extinction: the last may have been at least partially caused by the first two (McLeod *et al*., 1997). About 50% of species of major fossil clades were lost. Fish, however, appear relatively unaffected, with 90% of the chondrichthyan and 80% of the teleostean families surviving into the Tertiary (McLeod *et al*., 1997). In the context of freshwater fish, this crisis was even less severe, with estimates of only 10% of freshwater teleost families lost (Robertson *et al*., 2004). Concerning the Afro-Arabian freshwater ichthyofauna, the fossil record is too poor to comment on the turnover that may have occurred at the K/T boundary. However, the fish that inhabit Afro-Arabia since the Palaeocene (65.5 Ma-55.8 Ma) all belong to modern orders, with the exception of pycnodonts, an extinct group of basal actinopterygians that survive for some time in the Tertiary (for details, see Longbottom, 1984).

During the Palaeocene and the Eocene, Afro-Arabia is still a continental plateau with little significant topographic relief, worn down by erosion during a long period of tectonic stability. On this rather flat plateau, the watersheds between drainage systems were probably lower than today, which may have favoured faunal exchanges between basins (Beadle, 1981). This may explain part of the homogeneity observed within the modern African fish fauna (Greenwood, 1983), and also the similarities between several Afro-Arabian fossil ichthyofaunas that occur at the familial level and even at the generic level in certain cases (e.g., Otero, 1997; Otero and Gayet, 2001). Moreover, during most of the Palaeogene, great transgressions reach +200 m. This high sea-level regime stops at the Eocene/Oligocene (Fig. 1; Haq *et al*., 1987).

Then, during the Oligocene (33.9 Ma-23.0 Ma) and the Neogene (23.0 Ma to present), tectonic activity and anorogenic crustal movement markedly affect the African topography. The relative drift of the Afro-Arabian and Eurasian plates results in their collision, which corresponds to the Alpine orogenesis cycle. Dominant compressive tectonic phases drive the uplift of the Atlas Mountains in Maghreb since the Late Oligocene (Piqué *et al*., 2002) and of the Anatolian and Iranian mountains along the north-east border of the plate, during the Neogene (Thöny *et al*., 2006). They are the only Cenozoic compressional mountains of the Afro-Arabian plate (Figs 1, 2). Together with the Alpine compressive tectonics in the north and the extensive rifting tectonic in the east, Neogene mantle plumes (intra-plate hot-spots) largely contributed to the development of the basin and intra-continental swell topography, notably in Northern, Western, and Central Africa (Fig. 2; King and Ritsema, 2000; Goudie, 2005). The stratigraphic successions in the Sahara indicate rather warm temperature (Swezey, 2009). Elsewhere in Afro-Arabia, intra-plate extensive tectonic activity takes place in the east, along a roughly north/south axis. As a consequence, aligned rift basins open diachronically and separate new plates (Fig. 2). To the north-east, the partial dislocation of the Afro-Arabian plate started with the opening of the proto-Gulf of Aden at the very beginning of the Early Oligocene (Platel and Roger, 1989). From the end of the Early Oligocene to the Early Neogene, the rifting became stressed,

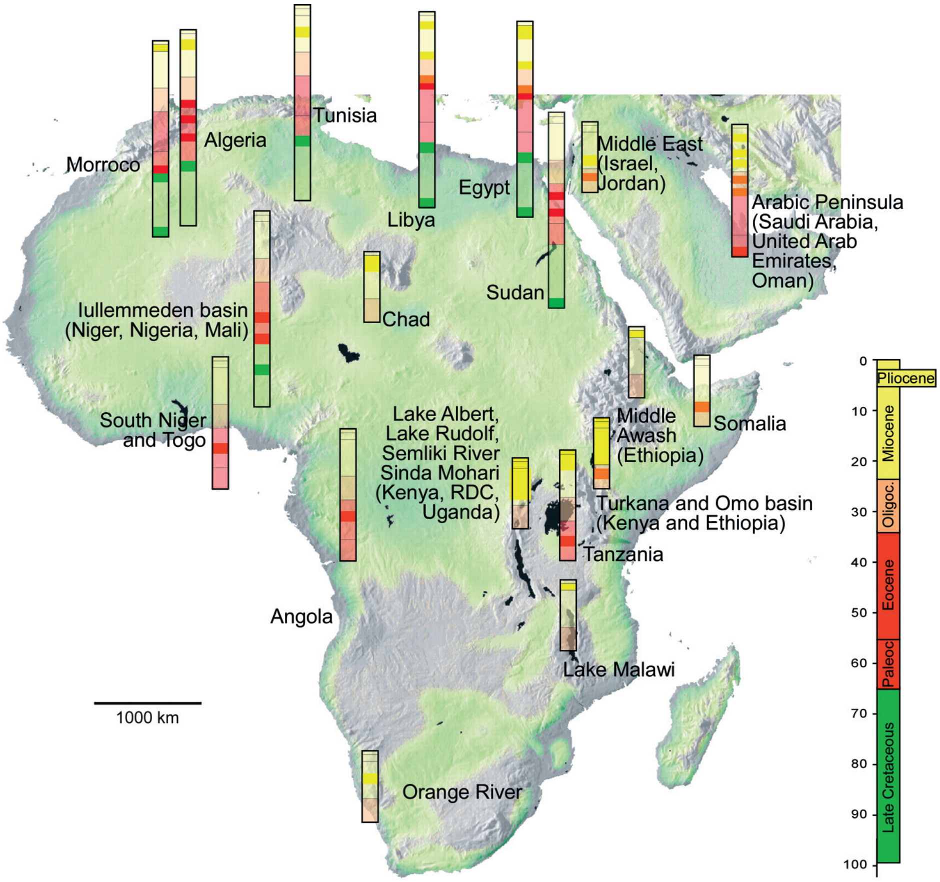

Figure 3. - Distribution in time and space of the outcrops that yielded freshwater fish fossils from Afro-Arabia aged 100 Ma and less. Ichthyological data from Adaci *et al.*, 2007; Arambourg, 1947, 1952, 1961; Arambourg and Joleaud, 1943; Arambourg and Magnier, 1951; de Broin *et al.*, 1974 ; Brunet *et al.*, 2000; Cappetta, 1972; Cappetta *et al.*, 1978; Casier, 1957; Churcher and Iullis, 2001; Dartevelle and Casier, 1949, 1959; Ducrocq *et al.*, 2010; Dutheil, 1999a, 1999b; Estes, 1969; Feibel *et al.*, 1988; Forey and Grande, 1998; Forey and Young, 1999; Gaudant, 1987; Gayet and Meunier, 1996; Gayet *et al.*, 1988; Gayet and Werner, 1997; Greenwood, 1951, 1959, 1960, 1972, 1973, 1974, 1987; Greenwood and Howes, 1975; Greenwood and Patterson, 1967; Longbottom, 1984, in press; Mahboubi *et al.*, 1986; Mannaï-Tayech and Otero, 2005; Martin, 1983, 1984a, 1984b, 1995, 1997; Micklich and Roscher, 1990; Murray, 2000b, 2003a, 2003b, 2004; Murray and Attia, 2004; Murray and Budney, 2003; Murray and Stewart, 1999; Murray and Wilson, 2005; Murray *et al.*, 2005, in press; Otero, 1997, 2001, 2003; Otero and Gayet, 2001; Otero *et al.*, 2006, 2007, 2008b, 2009a, 2009b, 2010, in press, unpublished; Patterson and Longbottom, 1989; Peyer, 1925, 1928; Pinton, 2008; Pinton *et al.*, in press; Priem, 1897, 1905, 1914, 1920; Schall, 1984; Schwartz, 1983; Stewart, 1990, 1994, 1997, 2003a, 2003b; Stewart and Murray, 2008; Stromer, 1905, 1910, 1914, 1916, 1936; Tabaste, 1963; Van Couvering, 1972, 1977, 1982; Van Neer, 1992, 1994; Weiler, 1926, 1929, 1935, 1970; Werner, 1993, 1994; Werner and Gayet, 1997; White, 1926, 1934, 1937. To limit the number of citation, when data are redundant in several papers, the ichthyological papers (where the fossil fish fauna is studied and new taxa are described) are cited rather than papers that present preliminary faunal lists.

the southern edge of the Arabian plate collapsed, and the oceanic crust appeared in the Gulf of Aden (Lorenz *et al.*, 1993; Platel and Roger, 1989). The dislocation of the Afro-Arabian plate sped up and the collision with Eurasia started during the Miocene. Rifting followed, albeit on a weaker scale, in the Suez and the Red Sea areas, pulling the African and the Arabian plates apart, while marine passage between the Mediterranean Sea and Indian Ocean across the Persian Gulf ceased (Fig. 2, Orszag-Sperber *et al.*, 1993). To the south, the East African Rift opening started in the Oligocene but the continental break-up stage has not yet been reached in that area. A series of more or less old deep lakes collapse diachronically along the rift axis and the opening seems to propagate from north to south (Woldegabriel *et al.*, 1990; Ebinger *et al.*, 1993; Van Der Beek *et al.*, 1998; Georges *et al.*, 1998; Delvaux, 2001; Chorowicz, 2005), which leads to complex drainage modifications throughout the Oligocene and the Neogene (e.g., Goudie, 2005; Chorowicz, 2005; Tiercelin *et al.*, 1988, 1992; Holzförster and Schmidt, 2007). Great modification would notably affect the Nile basin that really installs and possibly replaced a former east/west dominant flowing system (McCauley *et al.*, 1982, 1986). The existence of such a system has been contested by Burke and Wells (1989) but it fits with a certain fossil fish distribution (Otero *et al.*, 2009a). Finally, the rifting tectonics also affected the direction of the Congo River that evolved from an endoreic system to an Atlantic open basin in the Neogene (e.g., Lucazeau *et al.*, 2003; Séranne and Anka, 2005; Stankiewicz and de Wit, 2006).

The Neogene (23 Ma to present) has for a long time been recognized as the epoch during which the modern world emerged, including the transition from a warm Miocene to a cold Pleistocene with the growth of the polar ice-sheet and the plate motion creating the present day palaeogeographic configuration (Kennett, 1995; Burckle, 1995). The Early Neogene connection with Eurasia permitted the passage of fish that will further diversify in Africa and in Arabia, such as cyprinid fish that are first recorded in Afro-Arabia at 18 Ma (see Otero, 2001). Finally, the Late Neogene also registered drastic environmental changes with the onset of the Northern Hemisphere glacial cycle associated with quick climatic and eustatic oscillations (Haq *et al.*, 1987). This led to an increase in the seasonality and in the development of extreme environments in Africa and in Arabia, including the well documented increase in aridity in Eastern Africa (e.g., Levin *et al.*, 2004; Bobe, 2006) controlled by the climate change and the tectonic uplift (e.g., Bonnefille *et al.*, 2004; Demenocal, 2004; Sépulchre *et al.*, 2006). In Central Africa (Chad), the earliest trace of the Saharan desert is registered ca 7 Ma (Schuster *et al.*, 2006). Around the Mio-Pliocene boundary, the Mediterranean zone suffered the Messinian Salinity Crisis, an environmental event that affected the marine area and also the continental borders. This salinity crisis is known to have impacted the climate and provoked aridity in the terrestrial environment in the east of the Mediterranean Sea (Fluteau *et al.*, 2003; Fauquette *et al.*, 2006; Zazzo *et al.*, 2002). The combined effects of the Saharan development and the continental aridity linked to the salinity crisis possibly affected the Afro-Arabian freshwater ichthyofauna still present in the Middle and Late Miocene in Magreb and Mashreq (Otero and Gayet, 2001) and possibly favoured its replacement by the modern fauna dominated by European taxa. However, the dynamic of this replacement needs to be studied further to support this hypothesis.

Indeed, during the last 35 Ma, climate change and geodynamics fundamentally redrew the Afro-Arabian intra-continental basins and their environments. This time period also covers the diversification of the modern fish genera (Stewart, 2001; Otero and Gayet, 2001). Based on the spatial arrangement of the modern African freshwater fish, evidence of a regional pattern of the distribution structure in the ichthyological fauna arose at the beginning of the last century. At a continental scale, ichthyologists have attempted to identify ichthyological provinces, of which twelve are currently recognized (Lévêque, 1997). Numerous historical studies deal with the faunal affinities among these provinces (e.g., Boulenger, 1905; Pellegrin, 1912; Poll, 1957; Roberts, 1975; Hugueny and Lévêque, 1994) but few are considered in a phylogenetic framework, and thus they lack accurate dating of diversification events and their correlation with environmental change. Indeed, many African freshwater fish phylogeography studies focus on Great Lake fish history, and particularly on cichlids. On the contrary, larger geographic scale studies dealing with taxa widespread over Africa in several basins remain rare. A recent study dealing with catfish *Synodontis*, a widespread African genus, allows for the first time correlations between an African fish group history and environmental changes at the continental scale (Pinton, 2008). The results support the hypothesis that Oligocene and Neogene geological and climatic changes that dramatically affected the drainage systems in their shape, connectivity, and environment structured the diversity pattern of modern fish in Africa. Among others, three events in the evolutionary history of *Synodontis* can be related to a different environmental frame (Pinton, 2008). (1) The most ancient lineages of *Synodontis* are founded in the Congolese basin which supports the assumption made by Fjeldsa and Lovett (1997) that, due to their stability, forest areas enable survival of ancient lineages. (2) Middle Miocene vicariance between the eastern and the western parts of the Nilo-Sudan province correlates the rifting link remodelling of the hydrographical system in Eastern Africa. Based on palaeoichthyological evidence, Otero *et al.* (2009a) also concluded that prior to 7 Ma, allopatric speciation in the Chadian and Eastern African areas suggests a split within the Nilo-Sudan province in association with rifting. (3) Plio-Pleistocene climatic fluctuations favoured fish exchanges during wet periods between the Nile and the Chad basin and along the Western African coast.

THE DATA: THE AFRO-ARABIAN FISH FOSSIL RECORD OF THE LAST 100 MA

History of the description of the freshwater fish fossil record

Because there is a long history of fossil discovery and palaeontological study in Africa and Arabia, there is a large volume of literature on the subject. The aim here is not exhaustiveness but to sketch the global frame within which Afro-Arabian palaeoichthyology has developed over a century. The research has developed through three main phases over the last century (most of the available references are given in the caption of Fig. 4). A first “historical” phase took place from the early 1900s until the Second World War, providing preliminary faunal lists and first descriptions of fossil fish taxa and fish assemblages from regions that are generally still prospected today. They were, notably, Peyer, Priem, Stromer, and Weiler in Egypt, and White in Nigeria and Uganda. After the war, a second phase started slowly and developed further during the 1960s and 1970s, with

Arambourg in Ethiopia and Libya, Casier in RDC (République Démocratique du Congo), and then Greenwood in Arabia, Egypt, Kenya, RDC, Tanzania, and Tunisia. In 1974, Greenwood provided the first review of the African fossil freshwater fish record and Van Couvering added some new data in 1977. Then, in the late 1990s, African palaeoichthyological research saw the start of the current phase of studies, notably with Murray (in Egypt, Ethiopia, Kenya, and Tanzania), Stewart (in Ethiopia and Kenya), and Otero (in the Levant, Arabia, and Oman, and in Chad, Egypt, Libya, and Tunisia), and more recently Pinton. They have mainly focused on Tertiary outcrops so far. To these, I have to add Cavin and Dutheil, who focused on the Cretaceous Moroccan assemblages from the Kem Kem, Werner and Gayet, who gave interest to Cretaceous assemblages from Sudan (Wadi Milk) and Niger (In Becetem), Cappetta, Longbottom, and Forey, who concentrated on the Iullemmeden Basin, Van Couvering and Schwartz, who studied fish from Neogene outcrops in Eastern Africa, and finally the archaeo-ichthyologist Van Neer, who studies Pleistocene and Holocene fish assemblages including some from the Nile area and from the Sahelian zone in Africa, and also made some incursions in palaeontology, notably in the Mio-Pliocene of Uganda. Current studies mainly deal with material collected recently from historical outcrops (for instance, in Egypt) and from the newly discovered fossiliferous area (notably in Chad), and also from the review of historical material deposited in museum collections in Africa, Europe, and North America. The two last published reviews of the African fossil fish record concerned, respectively, all the Phanerozoic except the Neogene (Murray, 2000a) and the Neogene only (Stewart, 2001). Complementary data on the Arabian Tertiary fish record are to be found in Otero and Gayet (2001).

The freshwater fish record and the reliability of the dataset

Through discussions with A. Murray (University of Alberta) and K. Stewart (Canadian Museum of Nature), I felt that we delimit similarly the taxa in an assemblage. So, I consider that the number of taxa identified by different researchers in a given assemblage would be the same or close, which means that the fish richness (number of taxa identified) recorded in the different sites is also comparable. However, this level of information (taxonomic diversity in each locality) is not necessary for the present study. Former studies suggested that the number of localities is a good proxy to estimate the quality of the continental record (e.g., Fara, 2001). So, here I use the dataset of the outcrops that yielded freshwater fish to describe the fossil records. From the amount of works that refer to Late Cretaceous and Cenozoic Afro-Arabian fish (given in the caption of figure 3), a rather rich record of outcrops placed in a relatively precise temporal frame is available (Fig. 3).

The distribution of the outcrops

Figure 3 shows the great heterogeneity in the distribution of the fossil fish outcrops in both time and space. They are mainly concentrated in the north-equatorial half of the African plate including the Arabian Peninsula, and the distribution of the sites is very uneven in time between the several regions (Fig. 3). To describe the distribution of fish-bearing outcrops in both time and space, I delimited groups that gather sites from contiguous areas in close environmental contexts at a very large scale (for instance sites with a coastal position formed during a single major eustatic cycle, or layers that were deposited in a peculiar tectonic regime in a given region). A posteriori (I read his paper when mine was already submitted), I realized that the groups that I delimited in the Sahara during the Tertiary correspond to groups of large sedimentary deposit types as described and figured by Swezey (2009), with the exception of Egypt during the Pliocene. The examples chosen in further case studies are picked up in the different groups in order to consider contexts that are as varied as possible.

Late Cretaceous fish outcrops are concentrated in Northern and Western Africa (Fig. 3). They are present in Algeria, Morocco, Tunisia, Libya, Egypt, and Sudan, which means along the northern margin of the plate, as well as in the multinational Iullemmeden Basin that develops in Mali, Niger, and Nigeria. When transposed in the Late Cretaceous configuration (Fig. 1, section "Context"), this corresponds to continental deposits along the coasts of the epi-continental sea that extended onto Africa during that global high sea-level period. The deposits are thus frequently intercalated with marine deposits (e.g. Dutheil, 1999b, in Morocco; Cappetta, 1972, in the Iullemmeden Basin). From that point of view, the Late Cretaceous outcrops constitute a rather homogenous group. These sites are also rather homogenous in their fossil fish content for the marine – Tethyan – fish and also for the freshwater ones (see Murray, 2000a, for details). That indicates rather continuous environments along the Western and Northern African coasts at that time.

The Palaeogene outcrops of Northern and Western Africa and those of the Arabian area (which was still part of a single plate with Africa) may constitute a second group that resembles the first one, due to close contexts of sedimentation onto continental coastal plains and basins during a general high sea-level epoch (Fig. 1, section "Context"). The proximity of the seashore is indeed particularly well registered in the Fayum deposits, where marine and freshwater levels intercalate. Those levels respectively exhibit dominant marine (notably sharks and rays) and freshwater fish (mostly actinopterygians), as observed in the Late Eocene El Birket Qarun Formation (Murray *et al.*, in press). The youngest outcrops that may be included in this second group are those from the Lower Oligocene of Egypt, Libya, and Oman (Fig. 3), which is the last period with high sea-level (+200 m compared to modern, Fig. 1). The similarities between the fish assemblages within this second group are remarkable, notably when comparing contemporaneous assemblages, for instance those of the Late Eocene from Egypt (Murray *et al*., in press) and from Libya (Otero *et al*., unpubl. data).

In the Neogene, Northern Africa (Tunisia, Libya, Egypt, Arabia) and Central Africa (Chad) saw river deltaic deposits along the seacoast for the former and fluvio-lacustrine deposits for the latter (endoreic basin). These outcrops resemble each other in the great dimensions of the flowing systems implied (e.g., Dubief, 1953, for Tunisia; Griffin, 2002, for Libya; Thomas *et al*., 1982, for Arabia; and Schuster, 2002, for Chad).

The fourth and last group includes outcrops related to the East African Rift (Fig. 3). They are roughly aligned along the rift valley borders, notably at the lake banks (e.g., Turkana, Albert), but also in ancient river beds (e.g. Semliki). The oldest outcrops are Eocene and they range up to the Pleistocene. The record starts diachronically depending on the area, in relation with the diachronism of the rifting activity along the valley (Fig. 2, section "Context"). One of the most interesting characteristics of these outcrops is that they belong to sub-continuous series that may range over millions of years, offering original records of evolution in a given basin over relatively long time intervals. For instance, the fossiliferous series in Turkana at Lothagam ranges from the Lower Nawata layers to the northern Kaiyumung deposits of the Nachukui Formation and covers a time span of about 7.4 Ma to 2.7 Ma (Leakey *et al*., 1996; McDougall and Feibel, 1999). Over 7,000 fossil fish elements were collected from Late Miocene and Pliocene strata at Lothagam. They show considerable change throughout the sequence (Stewart, 2003a). The southernmost outcrops are the Pliocene ones in Malawi (material under study). Within this group, crater lake sites stand apart because of their peculiar environment and reduced basin size. This is the case of the Mahenge outcrop (Tanzania), which formed in a crater lake in a kimberlite pipe.

Finally, Southern Africa and the Congo basins are mostly without freshwater fish fossils during the last 100 million years, with the exception of the mid-Miocene locality of Arrisdrift (Otero, 2003). Conversely, these areas have yielded marine fish in outcrops located along the occidental seacoast, but also diverse freshwater ichthyofauna in the Palaeozoic (e.g., de Saint-Seine, 1955; Jubb and Gardiner, 1975). Moreover, certain areas have yielded fossil fish in certain time periods only. For instance, Eastern Africa is well endowed for the Neogene only, and is rather poor in Palaeogene outcrops and totally depauperate of Cretaceous ones.

DISCUSSION: ENVIRONMENT AND FOSSIL FISH IN AFRO-ARABIA

I first consider the environment at the time of transformation of a fish community into a fossil assemblage in a sedimentary bed. Then, at a larger scale I pay attention to the processes that may favour or prevent preservation of the fossiliferous bed. In these two sections I present case studies to try to expose environmental contexts and their impact on the freshwater fish fossil record. The main factors that limit the access to the outcrops and more generally our knowledge of the fossil record are evoked in a third section.

The fossiliferous bed deposit

Continental fossiliferous outcrops sample various local environments, including coastal areas such as swamps, different sections of rivers, notably deltaic zones, and also flood plains and lakes. Lakes are very diverse depending on their size, depth, and slope (deep lakes with abrupt banks in rift systems and shallow lakes with smooth slopes in epi-continental lakes) and also depending on their inclusion in a wider drainage system (with volcano crater lakes on one hand and endoreic fluvio-lacustrine complexes on the other hand). Indeed, a wide range of combinations between those types of basin and hydrographical system exists, but when I consider the factors that play a role in shaping fossil deposits, few physical parameters can be retained. The first is hydrodynamism, including its strength and the variation in intensity and direction. The second is the sediment itself, notably the size of the grains, which correlates with the hydrodynamism in the water body section and with the nature of the rock in the drained basin. Comparison of two fossiliferous sites that differ in their hydrodynamism with assumed modern equivalents would help to evaluate the impact of the energy level on the fossil record. I chose two sites that have been extensively sampled to avoid related problems.

The first example is the Chadian fossil fish assemblage from the Late Miocene area of Toros-Menalla (Anthracotheriid Unit, 7 Ma), at site TM266, which has been extensively described and analysed (Fig. 4; Otero *et al*., in press). The deposit corresponds to a flood plain in a fluvio-lacustrine environment which suffers a moderate to high hydrodynamism with fluctuations in both time and space. The observed faunal diversity includes vertebrates only (e.g., Vignaud *et al*., 2002; Le Fur *et al*., 2009), with the exception of insect constructions (Schuster, 2002; Duringer *et al*., 2007) and silicified wood (Schuster, 2002). There are at least 21 fish species at TM266 (Fig. 4), including members of fossil genera (the characiform *Sindacharax* and *Bunocharax*, and the perciform *Semlikiichthys*), and fossil species in extant genera (the catfish *Auchenoglanis soye* and several *Synodontis* species). The other fish are either indeterminate in extant genera or refer to modern species. They are bichirs (Polypteridae:

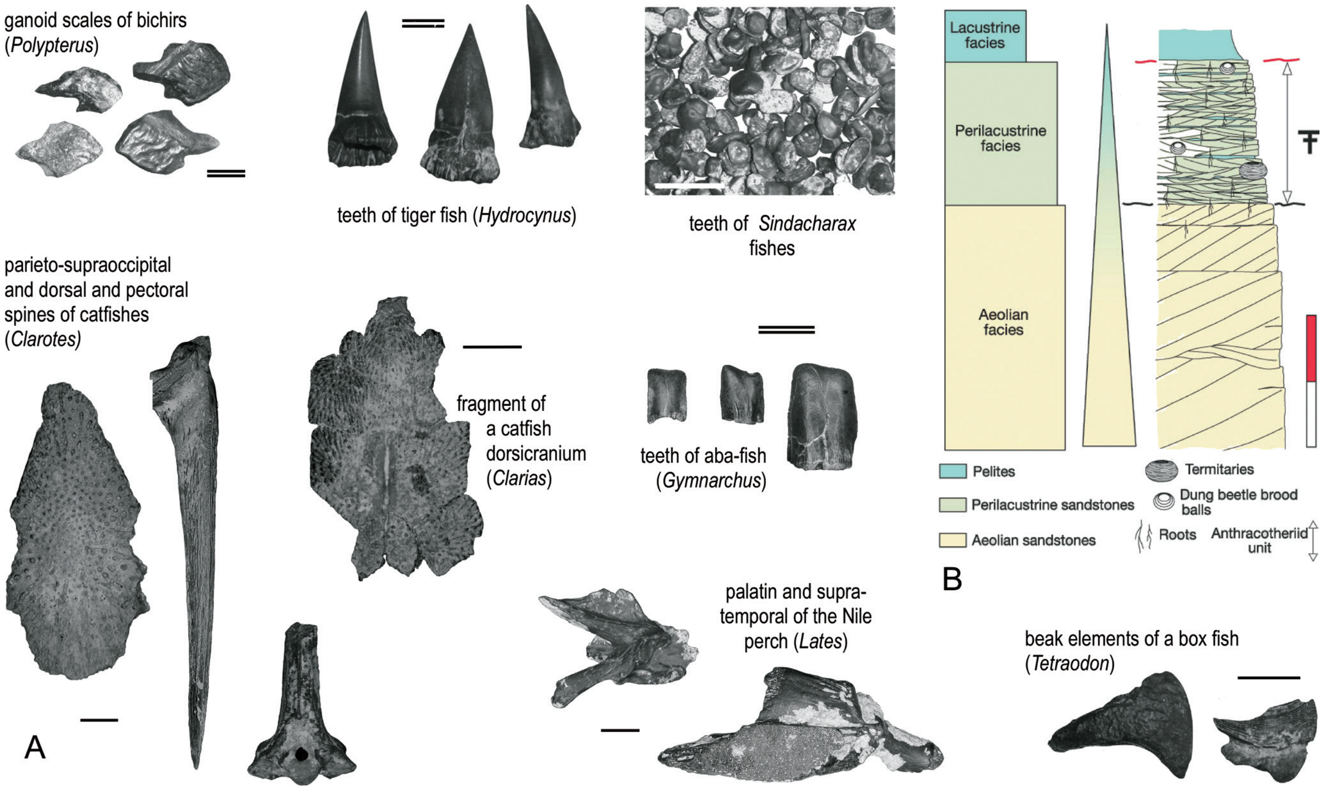
ganoid scales of bichirs (*Polypterus*)
teeth of tiger fish (*Hydrocynus*)
teeth of *Sindacharax* fishes
parieto-supraoccipital and dorsal and pectoral spines of catfishes (*Clarotes*)
fragment of a catfish dorsicranium (*Clarias*)
teeth of aba-fish (*Gymnarchus*)
palatin and supra-temporal of the Nile perch (*Lates*)
beak elements of a box fish (*Tetraodon*)
A
Lacustrine facies
Perilacustrine facies
Aeolian facies
Pelites
Perilacustrine sandstones
Aeolian sandstones
Termitaries
Dung beetle brood balls
Roots
Anthracotheriid unit
B

Figure 4. - The fish fossils and the outcrop in the Late Miocene of Toros-Menalla, Chad. **A**: Example of fossil fish remains (from Otero *et al*., in press). **B**: Stratigraphic column in the Anthracotheriid Unit showing the transgressive sequence that includes the fossiliferous bone bed (from Vignaud *et al*., 2002).

Polypterus sp.); osteoglossid fish (cf. *Heterotis niloticus*); aba fish (Gymnarchidae: cf. *Gymnarchus niloticus*); mud fish (Cyprinidae: cf. *Labeo* sp.); two types of extant alestid genera, which are a tiger fish (*Hydrocynus* sp.) and a tetra fish (*Alestes*/*Brycinus* sp.); and several catfish, among which are bagrids (cf. *Bagrus* sp.), claroteids (cf. *Clarotes* sp.), clariids (two *Clarias* sp.), and mochokids (two *Synodontis* sp.); the emblematic Nile perch is also present (*Lates niloticus*), together with indeterminate cichlids and two puffer fish (*Tetraodon* sp.).

Like in most fossil assemblages, the observed diversity is a fragmentary view of the past diversity that really existed. If we expect a past taxonomic diversity close to the modern one observed in the Chad basin (about 140 fish species today; Froese and Pauly, 2009), the "lost part" appears to be great here. Effectively I suspect that at 7 Ma the basin showed a fish diversity that falls in the same range as today or an even more diverse one, if the Saharan development and climatic oscillation effectively diminished the ichthyofauna in this endoreic basin. Indeed, this assumption is supported if we examine the skeletal pieces that have been preserved to define the factors that destroyed so many fossil remains (Otero *et al*., in press). The smallest remains that belong to minute taxa such as cyprinodonts are absent (or unsampled). This is also the case of fragile bones and minute teeth, which might explain for example the lack of many taxa in the faunal list such as mormyrids. On the contrary, the catfish that have strong dermal ossifications preserve well, as do large species with stout bones like *Lates* and those with large teeth (like *Hydrocynus*) or large tooth plates like *Tetraodon* (Fig. 3A). Moreover, the remains when they are preserved do not all carry precise taxonomic information and another part of the diversity is lost here. In the case of TM266, this explains the many determinations at a generic or family level, which might include specimens of different species.

The second example is the fossil fish assemblage discovered in Mahenge and dated at 45 Ma (Middle Eocene). This outcrop corresponds to crater lake deposits in a low energy context. Thousands of fossils were collected, including vertebrates, invertebrates (mainly arthropods, Harrison, 1997; Harrison *et al*., 1998), plants and fossil legumes (Herendeen and Jacobs, 2000; Jacobs and Herendeen, 2004). The site has been excavated by several teams and the fish have been studied by different authors. The taxa described so far are two osteoglossiforms (Greenwood and Patterson, 1967; Murray and Wilson, 2005), one clupeiform (Greenwood, 1960), one gonorynchiform (Davis *et al*., 2008), two characiform fish (Murray, 2003a, 2003b), one siluriform (Murray and Budney, 2003), and five cichlid species of a single fossil genus (Murray, 2000b). The fossils are articulated, generally lying on the flank.

In modern crater lakes, fish diversity is rather low. For instance, Schliewen (2005) signalled 15 species in the one million year old lake Barombi Mbo (Cameroon), twelve of which are endemic. Interestingly, the modern lake Barombi Mbo offers one of the few widely accepted examples of sympatric speciation, with cichlid species flocks according to Schliewen (2005). By comparison between the Mahenge fossil assemblage and the Barombi Mbo modern community, the fish and more generally the animals and bank plants appear to be rather well registered in the fossil crater lake. Indeed, this well documented fossil assemblage supports accurate palaeoenvironmental reconstructions notably inferred from the well preserved vegetation (e.g., Jacobs and Herendeen, 2004), and the cichlid diversity observed there suggests that these fish already evolved the ability to form species flocks as early as the Eocene (Murray, 2001). The apparently high quality of the taxonomic diversity revealed (probably close to reality) is due to the fact that most taxa are documented (no selective destruction of certain taxa remains due to their size and stoutness) and also to the fact that fish were preserved articulated, which allows precise taxonomic attribution, generally at a specific level.

The fish assemblages preserved in these two fossil outcrops are registered at different epochs, explaining why many more extinct taxa are present in Mahenge. More interestingly, these two different lacustrine or peri-lacustrine environments registered different diversity patterns of the ancient fish communities in relation with the drainage system characters. There were and still are relatively few species in many genera in the old and great Chadian basin, whereas there were relatively many species within few genera in the relatively short life and surface limited fossil Mahenge crater lake like in the modern lake Barombi Mbo.

As for any fossil, the preservation characteristics vary depending on the hydrodynamism of the environment. The lower the energy level, the better the fossils are preserved. In the crater lake, a larger part of the diversity appears to be preserved, including minute species. Moreover, the level of determination is more accurate, and closely related species are distinguished. Indeed not only are vertebrate bones and teeth fossilized there but also delicate tissues are preserved, like chitin (arthropods) or cellulose (plants). On the contrary, the number of diagnostic features diminishes as hydrodynamism increases. For instance, meristic characters disappear when the fish disarticulate and the identification of isolated remains becomes harder as the remaining fossils lose their finest structure (by weathering). However, these observations from our case studies have to be moderated by others that illustrate how high hydrodynamism can favour the record of fossils. Indeed, high hydrodynamism may offer the advantage of concentrating fossils in some layers (for an example see Otero *et al.*, 2009a). It may also play a role in the transport of the fossils before the deposit and thus eventually induce mixing of remains of fish from different areas in a hydrographical network.

Low energy environments are rare and cases such as the crater lake at Mahenge are exceptional in continental areas. The discovery of such sites offers unique opportunities to discuss evolutionary processes in the fossils such as the cichlid flocks (Murray, 2001). Together with low hydrodynamism, early diagenetic processes (e.g., rapid burial by thin sediment layers, cover by a bacterial film, or anoxic conditions in lake bottoms) can permit the preservation of organic tissues. Certain diagenetic processes may favour one or another type of mineral tissue remains due to their chemical composition. For instance, bones and otoliths are rarely found together, whereas teeth and bones may be found in the same beds. Some diagenetic environments preferentially preserve phosphate alone (bone and tooth apatite), whereas others also preserve carbonates (otoliths). This influences the taxonomic diversity observed since an open nomenclature exists for the otoliths. Lastly, exceptionally one may find a site with exceptional preservation in a large drainage system basin. For instance, in the case of the Chadian fossiliferous area, most outcrops resemble the locality TM266 and yield disarticulated remains, except a few sites where articulated fossils can be collected, such as the holotype of a fossil bichir species (e.g., Otero *et al.*, 2006). In that case, the outcrop probably corresponds to a dried swamp.

To conclude, on the continent, the depositional environments are various and rather fragmented. They strongly control the freshwater fish fossil record. Understanding the sedimentary deposit dynamic and taphonomy of the fossiliferous bed is central to interpreting the fossil diversity observed in an outcrop. It is notably necessary to evaluate the space and time averaging of the fossiliferous layer and the sort that affected the fossils to know which part of the diversity is preserved.

The record of the sedimentary archives

At a larger, regional scale, I question here the impact of the base level height and its variation on the preservation of the deposits and thus on the shape of the freshwater fish fossil record. Former studies have shown the fundamental role played by sea-level variations in shaping diversity patterns in the marine fossil record, by controlling taphonomic mega-biases and surface outcrop area (e.g., Smith, 2001; Smith *et al.*, 2001). Intuitively, one may speculate that sea-level would also control the terrestrial fossil record by modelling continental depositional environments favourable to fossilization, for instance by increasing the continental area available at low sea-level (notably coastal plains). However, intuition may also lead to an opposite conclusion, because sea-level not only controls the surface available for outcrops, but also controls the range of erosion of the deposits on the continents according to the continental surface and reliefs exposed. When considering this second aspect, a low sea-level will induce an increase in erosion, which means fewer fossiliferous outcrops. Indeed, during the sea-level fall, the sedimentary and fossiliferous material is particularly susceptible to being reworked and the potentially preserved deposits are displaced sea-ward in the basin. The part of each aspect of this possible antithetic effect of sea-level change on the preservation of freshwater fish outcrops is hard to estimate and here again I would concentrate my efforts on case-description. To take into account the whole range of continental basins (e.g. sea coast basins, endoreic basins, rift basins) and the different types of control on their sedimentary environments and their preservation through time (e.g., tectonics, sea-level, climate), I shall use the concept of accommodation – free space available for sedimentation between the base level and basin bottom – which directly controls the distribution of depositional environments in any basin (Guillocheau, 1995). For fossil fish outcrops, I retain three cases in different geomorphological contexts, in both anorogenic and orogenic regions.

First, there are outcrops that border the sea coasts, where the depositional environments exist in an anorogenic context – I exclude the case when tectonics, such as the Atlas orogenesis, affects the sea coast locally. The base level corresponds to the sea-level and variations in accommodation are mainly controlled by eustasy. The Cretaceous and Palaeogene seacoast outcrops that yielded freshwater fish are numerous. Indeed they constitute most of the freshwater fish record of Afro-Arabia during these periods, which correspond to general high sea-level periods (my groups 1 and 2). Moreover, they generally appear to have formed during episodes of sea-level rise. For instance, the Cenomanian high sea-levels are the highest ever registered in the Phanerozoic, and the Cenomanian also corresponds to the Late Cretaceous richest time period for coastal freshwater fish sites in Africa (Figs 1, 3, and related text). In detail, the Continental Intercalaire corresponds to continental deposits that preceded the Cenomanian transgression in the upper part of the Lower Cretaceous (Albian and Aptian) and the very beginning of the Upper Cretaceous (Cenomanian); they consist of continental sandstones in Northern Africa (Mateer *et al.*, 1992). The Cenomanian deposits that yielded freshwater fish are frequently intercalated with marine dominant deposits (e.g., Dutheil, 1999b, in Morocco; Cappetta, 1972, in the Iullemmeden Basin). In the Kem Kem for instance, they lie just under Late Cenomanian marine transgression carbonates (Forey and Grande, 1998; Dutheil, 1999b). Interestingly, several authors noted that the Cenomanian-Turonian sea-level high stand is accompanied by a globally depauperate continental fossil record in the case of tetrapod vertebrates (Benton, 1989; Fara and Benton, 2000; Fara, 2002). Conversely, in the case of Afro-Arabian freshwater fish, at least certain transgressive episodes appear to have favoured the freshwater fish fossil record, possibly through enhancing the preservation of coastal plain deposits.

Second, in the case of fluvio-lacustrine environments in endoreic basins, the base level depends on the water balance and the topography of the basin. The accommodation variation depends mainly on the hydrographical variations through time. Although rather uncommon on other continents, endoreic basins are numerous in Africa and were even more frequent during certain periods in the past. The Chadian endoreic basin was set up in the Tertiary between the emerging Ennedi (east), Tibesti (north), and Cameroon (south-west) plumes and the pre-existing African Central Shear zone (south). The fossiliferous deposits consist mainly of siliciclastic series dominated by weakly lithified sandstone interbedded with argillaceous mudstones and diatomites (Schuster, 2002). The fossiliferous layers are root-rich perilacustrine deposits characterized by the mixing of both inherited Aeolian sand and other grains resulting from the reworking of lacustrine sediments (Schuster, 2002). They have yielded thousands of vertebrate remains, notably fish, common fossilized dung beetle brood balls, and rare termitaries, in four areas ranging from the Late Miocene to the Early/Late Pliocene. In Toros-Menalla (the oldest of the four areas, see Fig. 4), the fossiliferous beds overlie the oldest known fossil Aeolian dunes of the Sahara (Schuster *et al.*, 2006). The fossiliferous layers are covered by a lacustrine series that has also yielded some rare fish fossils. These layers correspond to shallow perilacustrine environments, which were subject to frequent inundation due to recurrent lateral variations of the shoreline, change in the stream path and seasonal flood. The sequences that contain the fossil fish beds are transgressive (Fig. 3B). They start with desert dune environments, at least in Toros-Menalla, and finish in diatomitic deposits of high lake level (Vignaud *et al.,* 2002). Here, the control of the sedimentation is clearly climatic, through the water input and balance in the Chad drainage basin.

Finally, in tectonically active regions, the main difference from the former cases is that tectonics controls accommodation, rather than eustasy or climate. Thus, a main trend dominates the accommodation variation through time as long as the constraint remains locally. Typically, in the Eastern African Rift region, the deepening of basins during several millions of years allowed the deposit of hundreds of metres of sediments in freshwater lakes and neighbouring fluvial systems thanks to the sub-continuous formation of free space for sediment deposits. In that case, there are sub-continuous sedimentary series in the rift grabens. They show diachronic opening and deepening, the oldest being Palaeogene, while sediments still accumulate in modern lakes. From north to south, great time periods of the African fish history are registered. The study of this record permits a high-resolution perception of the freshwater fish diversity and evolution during relatively long time periods in a given basin. For instance, the exhaustive study of the Turkana series at Lothagam (Stewart, 2003a) and at Kanapoi (Stewart, 2003b) provides rare information on certain species' evolution; for example, five species of the fossil *Sindacharax* genus were present in the Late Miocene to Pliocene-aged deposits at Lothagam and they show different associations in that time span (Stewart, 2003a).

To summarize, Afro-Arabian freshwater fish outcrops are globally associated either with marine transgressive time periods (the case of the Cenomanian Northern African sea coast deposits), with freshwater transgressive contexts in endoreic basins (the case of the Miocene Chadian outcrops), or with the deepening of the basins in a rifting context (the case of the Late-Palaeogene to Recent fossil beds in the East African Rift Valley). These cases cover the main types of basins present in continental Africa. Through their overview, it seems that change in the base-level deeply influences the continental fish fossil record, in relation with sedimentary dynamics (rate of preservation/erosion of the deposits), rather than the base-level itself (which defines the available continental surface). Such a direct control by the sequence stratigraphy on preservation of vertebrates has ever been described in details for a marine assemblage (Eocene of Egypt; Peters *et al.*, 2009) and for both marine proximate and terrestrial environments (Cretaceous of Montana; Rogers and Kidwell, 2000).

The controls on accommodation, that is, eustatic, tectonic, climatic, and sedimentary input, depend on the basin considered, and the rhythm and tempo of its variation will differ dramatically according to the context (Guillocheau, 1995). However, in all three cases studied, an increase in accommodation appears to have favoured the preservation of freshwater fish outcrops. Indeed, in the case of coastal deposits and endoreic basin, the freshwater fish fossiliferous beds correspond to layers that were deposited before transgressive maxima, where marine and deeper lake sediments were deposited, respectively. I may speculate that in endoreic basins the fossil record may be affected not only by changes in water balance (e.g. monsoon, seasonality, aridification trend), but also, over longer time scales, by the growth and erosion of the reliefs (including plumes) that border these basins. In the peculiar case of a rift, the deepening trend induces the deposit and favours its preservation, but the exact position of the successive fossiliferous layers in the sequences deserves accurate analysis. Finally, past base levels lower than the modern one may generate deposits mainly in zones that are now immerged if not uplifted by tectonics or isostasy.

Environments and the knowledge of the freshwater fish fossil record

By comparing the fossil assemblage in Toros-Menalla (Chad, 7 Ma) and Mahenge (Tanzania, 45 Ma) I evoked how the quality of preservation (articulation, weathering, etc.) depends at least partly on the sedimentary environmental energy which thus influenced the taxonomic level of identification. Indeed, the latter depends not only on the preservation, but also on the taxa itself (the diagnostic value of the remains that preserve) and on our ability to accurately identify the fossils. Thus we can enhance our knowledge thanks to the increase in our determination capacities. For instance, for a long time the fossil diversity of the catfish genus *Synodontis* was unknown, most of the fossil remains being attributed to *Synodontis* sp., with the exception of *S. frontosus* signalled in Pleistocene deposits in Eastern Africa. A recent study of the bony anatomy of eleven Chadian modern species (Pinton *et al.*, 2006; Pinton and Otero, in press) led to evaluating the fossil diversity at a minimum of five taxa in the Late Miocene of Chad (Pinton, 2008). The other way to increase the observed diversity in a site is related to the sampling methodology. Screening in the field allows small sized remains to be collected. The systematic information provided by the millimetre fraction is different and complements the information brought by macro elements collected at sight at the sediment surface (Murray *et al.*, in press; Otero *et al.*, 2009b, 2010, in press). I estimate that over one quarter of the fish diversity described in the Neogene Chadian fluvio-lacustrine deposits (Otero *et al.*, 2009b, 2010, in press) is due to screening below 4 mm. Indeed a sampling strategy has to be adapted according to the context and related preservation. Both these aspects are directly linked to scientific approaches and indicate that field studies in formerly examined sites and review of formerly studied assemblages should not be neglected.

Finally, regional geological history and modern environments facilitate or prevent the access to the outcrops and have to be taken into account when we wish to improve our knowledge.

By comparing the distribution of the sites and the modern topography of Afro-Arabia (Fig. 3), outcrop-rich areas appear concentrated in relief zones, whereas flat regions are relatively depauperate. Indeed, processes like folding, faults, linked horizontal and vertical movements of the crust, and strong erosion that greatly favour the access to ancient sedimentary archives preferentially occur in tectonically active regions, in both orogenic and rifting contexts. For instance, in the Rift Valley, the rifting mechanisms include a series of processes such as the deepening of the median basins, but also faulting, uplifting of the lips of the rift, and tilting of blocks, which bring to the free air cuts in ancient sedimentary series. The Eastern African series exposed are thus subcontinuous and cover several million years, as in the Turkana basin, for instance. Of course a variety of exceptions exist in

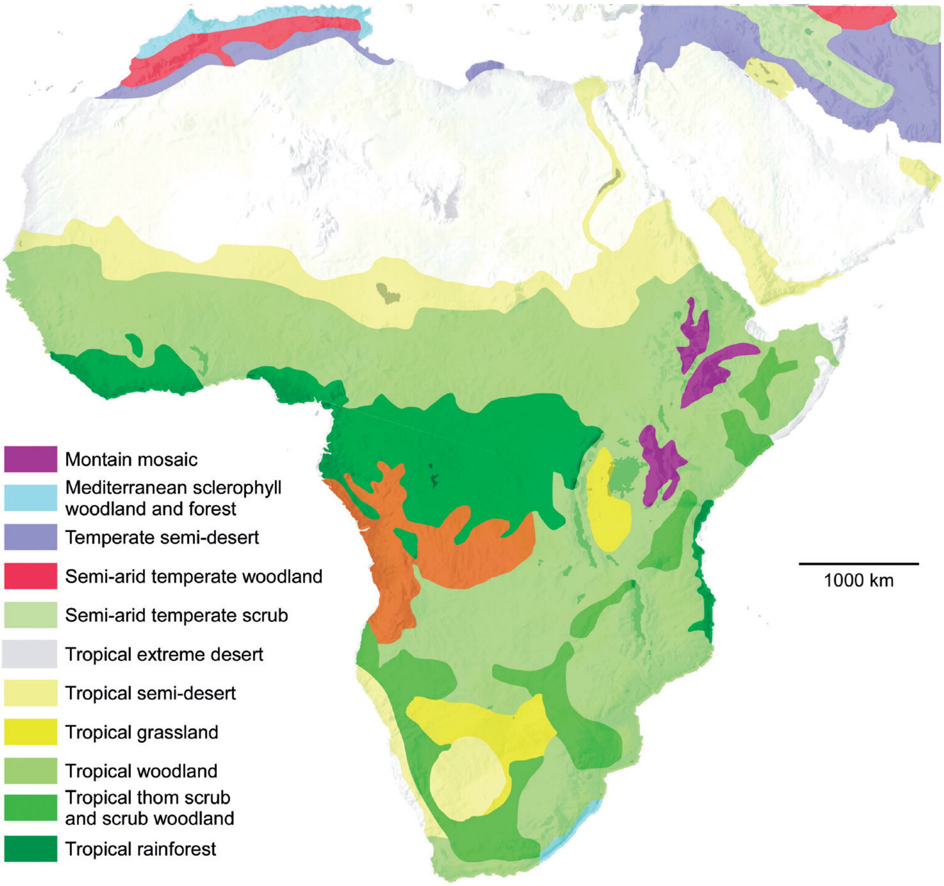

Figure 5. - Modern vegetation map of Africa.

relation to the many complex geological histories and local contexts. The extreme would be found in the Djurab desert (Southern Sahara, Chad), which offers four Late Neogene fossiliferous areas. In that case, the landscape is totally different: Aeolian erosion allows the deflation of sedimentary series that did not suffer any tectonic activity and remain tabular. In that context, erosion exposes wide and flat fossiliferous areas that correspond to short time windows.

Through a rapid comparison of the outcrop distribution (Fig. 3) and of the modern vegetation of Afro-Arabia (Fig. 5), the unsurprising pattern is that densely vegetated cover correlates negatively with the collection of fossil fish. In fact, sites are poorly sampled in the forest first because of the soil cover and also because certain forestry zones are depauperate and hard to access. That explains the scarcity of freshwater fossil fish sites in the Congo basin (Fig. 3). Contrarily, the discovery of sites is easier in open environments because reduced vegetation and soil cover do not hide the rock and are easier to access. In fact, the modern environmental and human factors are much more diverse and complex, as shown through the two following examples. First, we may know of fossiliferous outcrops in some areas with thick vegetation depending of the industrialization intensity and particularly the mining activity or the development of communication routes. Second, the population density may play a role and explains why fossils are rare from zones where people do not live or travel, such as the Arctic.

CONCLUSION

African ichthyology has a long history during the last century and the beginning of the current one. Some areas are still poorly known and require data collection (notably in the Congo Basin) and some African fish taxa require in-depth reviews (notably cichlids). But we already have a rather precise idea of extant fish diversity and distribution (e.g., Lévêque and Paugy, 2006) and the new interactive database Faunafri (Paugy *et al*., 2008) opens great perspectives in their study. However, the works on modern taxa alone are not sufficient to reconstruct the history of the African fish in its whole complexity, and reliable data on palaeodiversities and palaeodistributions are needed (and would include Arabian palaeontological information).

The progress made in taphonomy and stratigraphy allows deep advances in paleontological investigations and macroevolutionary history of marine animals by understanding the controls on their fossil record (e.g., Kidwell and Holland, 2002; Peters, 2006; Peters *et al*., 2009; Smith, 2007). However non vertebrate animals and terrestrial environments are neglected (Peters *et al*., 2009) and the fossil record of continental freshwater fish is underexplored. I started here a preliminary but compulsory work that aims at identifying the processes independent "from the fish itself" that shape the freshwater fish fossil record in continental Africa. Identification of these processes is all the more necessary as some also play on fish evolution such as the hydrographical network configuration. This work is also crucial if the aim is to use fish as proxies to reconstruct the history of drainage systems, which is itself the pure product of the environment on continental topography (tectonism, climate, eustasy).

If the fish fossil record clearly depends on the fish itself and its diversity, its distribution, and the species life duration, this review shows that a variety of environmental factors impact it and give it its final shape. These factors include taphonomy, sedimentary environments, erosion, and depositional processes. They are controlled by tectonics, climate, and eustasy but vary according to the place. Indeed, each region and even, at a lower scale, each area, will present its own environmental characteristics and a specific balance between the factors that shape the fossilization process and the fossiliferous layers record. The multiplicity of the factors and their strong variation over the continent and through time made it impossible to quantify their relative role in shaping the fossil record without an accurate choice of the outcrops compared. The present study may provide a first step guide to the choice of the cases to be studied to test the environmental factors separately. Notably, the precise study of fossiliferous series will allow the test of the observations summed up in the "Discussion", notably the fact that increase of accomodation seems to favour preservation. Moreover, two questions arose: 1) whether the fact that freshwater fish inhabit their fossil depositional environment modifies the impact of the environment on the fossil record when compared with terrestrial faunas, and 2) whether fish fossils and other freshwater animal fossils behave in the same way, which seems not to be the case in proximal marine environments (Rogers and Kidwell, 2000, Peters *et al*., 2009).

Besides shaping the freshwater fish fossil record, the environment can limit or favour the access to the outcrops, and then controls our knowledge of the fossil record. I have illustrated the great features of the regions where the fish fossils are frequently found so that part of fossil distribution can be easily interpreted. For instance, it explains that the lack of fossil *Polypterus* prior to the Neogene time (23Ma to present) in Eastern Africa is simply due to the lack of available outcrops for older time periods in this area, whereas *Polypterus* is known elsewhere since the Palaeogene, for instance in Northern Africa. One important issue is that the use of the fossil record cannot be considered alone to infer a taxon's history. The positive counterpart is that the time and space distribution of a given taxon of fossils compared with the outcrops available, including their environmental characteristics, may shed light on a change in the habitat or diversification event (Stewart, 2003a; Otero, unpubl. data).

In order to answer the remaining questions "How can we improve our knowledge on the fish fossil record in Africa? And thus on past diversity?" I propose three paths.

New excavations in historical outcrops and prospects of new outcrops that recorded common and rarer environments will provide new material and new taxa. The discovery of new outcrops and new fossiliferous layers is necessary, notably in zones were the freshwater fish fossil record is null or virtually absent. For instance, prospects in the Congo-Zaire Basin, in Southern Africa, and in far Western Africa may document great unknown pieces of the fish history.

The use of screening sampling methods in the field allows us to collect remains of small size that provide different and complementary systematic information when compared with surface collections (i.e., Murray *et al*., in press; Otero *et al*., 2009b, 2010, in press).

Finally, osteological studies of certain taxa will enhance the known fossil fish diversity, as suggested by current studies on *Synodontis* catfish (Pinton *et al*., 2006; Pinton, 2008; Pinton and Otero, in press).

Acknowledgements. - I gratefully thank Maarten de Wit (!Khure Africa) as the discussion we had in Paris probably caused the redaction of this paper, and also Aurélie Pinton for having read a previous version of this paper with great attention. I also extend gratitude to the reviewers for their comments and suggestions.

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